

**Evidence for Widespread Courtship During Copulation in 131 Species of Insects and Spiders, and Implications for Cryptic Female Choice**



William G. Eberhard

*Evolution*, Vol. 48, No. 3 (Jun., 1994), 711-733.

Stable URL:

<http://links.jstor.org/sici?sici=0014-3820%28199406%2948%3A3%3C711%3AEFWCDC%3E2.0.CO%3B2-C>

*Evolution* is currently published by Society for the Study of Evolution.

---

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/about/terms.html>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/journals/ssevol.html>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

---

JSTOR is an independent not-for-profit organization dedicated to creating and preserving a digital archive of scholarly journals. For more information regarding JSTOR, please contact [support@jstor.org](mailto:support@jstor.org).

## EVIDENCE FOR WIDESPREAD COURTSHIP DURING COPULATION IN 131 SPECIES OF INSECTS AND SPIDERS, AND IMPLICATIONS FOR CRYPTIC FEMALE CHOICE

WILLIAM G. EBERHARD

*Smithsonian Tropical Research Institute and  
Escuela de Biología, Universidad de Costa Rica,  
Ciudad Universitaria, Costa Rica*

*Abstract.*—Male courtship behavior is generally thought to function *prior* to copulation, as an inducement to the female to allow the male to copulate with her; this study indicates however, that male courtship *during and following* copulation (“copulatory courtship”) is common in insects and spiders (81% of 131 species in 102 genera and 49 families, mostly Coleoptera, Hemiptera, Diptera, and Araneioidea). Copulatory courtship is apparently evolutionarily labile, as expected if it is under sexual selection; intrageneric variation occurred in all 17 genera in which more than one species was observed. In 81% of 94 species with copulatory courtship, the male abandoned the female soon after copulation ended; thus, copulatory courtship appears not to function generally to induce acceptance of further copulatory attempts. The most likely explanation for copulatory courtship is that it represents attempts by males to influence cryptic female choice. This suggests that an aspect of sexual selection by female choice not considered by Darwin may be more important than previously appreciated and that the common practice in evolutionary studies of measuring male reproductive success by counting numbers of copulations may sometimes be misleading because of cryptic female choice during and after copulation.

*Key words.*—Copulation, courtship, cryptic female choice, insects, intrageneric variation, sexual selection, spiders.

Received March 12, 1993. Accepted June 14, 1993.

In his chapter on “Principles of Sexual Selection,” Darwin (1871) repeatedly referred to competition between male animals in terms of attempts to “possess,” “obtain,” or pair with females. The implication is that sexual selection acts on male abilities to gain sexual access to females. Subsequent studies of sexual selection through the present generally have maintained this emphasis (e.g., Bateson 1983; Bradbury and Andersson 1987). Indeed, the common understanding of male courtship behavior, which is often thought to be under sexual selection, is that “broadly conceived, [it] encompass[es] all behavior patterns of precopulation, pair formation, and pair bonding” (Immelmann and Beer 1989, p. 62).

This emphasis on the events leading up to copulation overlooks, however, the fact that copulation in animals with internal fertilization seldom leads directly and inevitably to fertilization of the female’s eggs (Eberhard 1985). Instead, even after copulation has begun, several processes that are sometimes or always under the direct control of the female can influence the chances that a given copulation will result in fertilization of her eggs. A possibly incomplete list includes premature interruption of the copula-

tion; granting of deeper genitalic access to internal sites where the male’s sperm will have a better chance of being used; sperm transport to storage and/or fertilization sites within the female; sperm nourishment; discharge or digestion of the current male’s sperm or those of previous or subsequent males; ovulation; preparation for implantation of embryos; oviposition; rejection or removal of mating plugs; and rejection of subsequent advances of other males (Thornhill 1983; Eberhard 1985, 1990, 1992, 1993). If females do not respond equally to all conspecific males in these processes, then “cryptic” female choice (Thornhill 1983) can occur (“cryptic” in the sense that even though a male was accepted as a partner in copulation, he may nevertheless be rejected as a father of the female’s offspring). These and other considerations (such as evidence for post-copulatory sperm removal, e.g., Waage 1983) imply that perhaps sexual selection is better understood as competition between males for access to females’ gametes rather than to the females themselves.

Cryptic female choice recently has been demonstrated in several species (van den Assem and Visser 1976; Thornhill 1983; Sivinski et al. 1984; J. Sivinski pers. comm. 1993; Alcock and Buch-

mann 1985; Otronen and Siva-Jothy 1991; Watson 1991). It is not yet clear, however, whether cryptic female choice is as widespread as some (Eberhard 1985) have suggested (Birkhead and Hunter 1990). Because numerous mechanisms exist by which females could effect cryptic choice, it is difficult to determine by direct observations whether it occurs in any particular species. It is possible, nevertheless, to use the male's behavior during copulation as a conservative assay to infer cryptic female choice. The reasoning is as follows.

If cryptic female choice occurs in a species, the males of that species will be selected to attempt to influence the female's choice by inducing her to perform the postintromission process or processes that will increase his chances of fathering her offspring. Any of several types of male behavior could be used: courtship before copulation (e.g., Crews 1987); genitalic stimulation during copulation (Eberhard 1985); or courtship during copulation (Eberhard 1991). Male courtship behavior that occurs after intromission already has begun ("copulatory courtship") should thus constitute a conservative indication that selection in the form of cryptic female choice may be acting on the males (Eberhard 1991). Just as the presumed function of male courtship behavior prior to copulation is to induce a female response favoring the male's reproduction (allow him to copulate), so courtship after copulation has begun probably also induces further female responses (sperm transport, etc.) which also favor his reproduction.

A previous compilation of 230 published accounts of mating behavior in insects showed that copulatory courtship is relatively widespread: in 36% of 302 species, 34% of 231 genera, and 43% of 102 families in 13 different orders, males apparently court females after copulation has begun (Eberhard 1991). Several reasons exist to suppose, however, that these frequencies are underestimates (Eberhard 1991). The object of this study is to obtain a more precise estimate by overcoming two potential biases in previous accounts: possible underestimates caused by the difficulty of observing behavioral details in some species, and lack of attention to male behavior during copulation.

#### MATERIALS AND METHODS

The species in this study were chosen mainly on the basis of ease of study. Only species in

which copulating pairs could be observed at close range (usually under a dissecting microscope) were included, and particular attention was paid to male behavior during copulation and immediately afterward. Most species were relatively common and copulated more or less readily in a confined space. I also sought to include a variety of taxonomic groups; thus, candidate species in families not yet studied were given preference. I chose some other species because I had already made observations of congeners in an attempt to assess whether copulatory courtship behavior shows relatively rapid divergence. No species was included if I had prior knowledge of whether copulatory courtship occurred (the only "exception" was the staphylinid *Leistotrophus versicolor*, which a previous publication had suggested might lack copulatory courtship, but which turned out to show it).

Criteria for deciding whether a given behavior should be considered "courtship" rather than attempts by the male to perform other functions such as maintain genitalic contact with the female, clean himself, or repel the advances of other males, were the following:

1. The behavior was repeated, in general outline if not in minute detail, both during a given copulation and in different copulations. In most cases, behavior that was not repeated rhythmically was not counted as courtship (e.g., footnote 59 in the Appendix).
2. The behavior was appropriate to produce stimulation of the female. For instance, waving legs that did not consistently touch the female and were out of her sight was not counted as courtship unless the movements were so energetic and jerky that they vibrated her body. Nearly all movements that were counted involved tapping, rubbing, or vibrating the female (see the Appendix). Movements that caused sexually dimorphic structures of the male (e.g., ventral hairs of *Scaphidopsis* beetles, modified abdominal sternites of *Phyllophaga* beetles) to rub against the female were counted.
3. The behavior was mechanically "irrelevant" to the male's problems of staying physically coupled to the female. Thus, for instance, I did not count movements of the male's legs associated with mechanical problems of alignment with the female as she moved, with pushing his genitalia deeper into her body, or with the approach of another individual.

4. The behavior was not performed in contexts suggesting other functions (e.g., cleaning movements or apparent threats elicited by the approach of other individuals were not included).
5. Thrusting and twisting movements of male genitalia were not counted as courtship, because in none of the species studied are the mechanics of copulation understood well enough to distinguish movements involved in sperm transfer per se (or possible sperm removal) from others. Not counting this very common type of rhythmic movement probably results in an underestimate of the frequency of copulatory courtship (Eberhard 1985). Rhythmic movements causing portions of the male genitalia to rub or tap on the *outside* of the female during intromission were counted (two beetle species, two hemipterans, one homopteran), as were rapid vibrations of the genital capsule, which caused the female's body to vibrate (two hemipterans).
6. Male behavior that, judging by the context, may have induced the female to refrain from capturing the male after copulation ended (two spiders) was not counted because such behavior may not influence female use of the male's sperm.

It should be kept in mind that definitive proof that a given behavior pattern functions as courtship requires demonstration that females respond to the behavior in ways that increase the male's reproductive success. Such data are lacking for the copulatory courtship behavior of the species described here (as indeed, they are absent for the overwhelming majority of species in which precopulatory behavior by males has been interpreted as courtship). The term courtship in the descriptions that follow should be understood in this tentative sense.

My observations of 17 species were complemented by more extensive observations by my students, and sample sizes in the Appendix include the students' observations. Video recordings were made of 13 of these species. A National Omnipro camera with +6 closeup lenses, or a CCTV camera coupled to a Wild dissecting microscope and a JVC HR-S8000U SVHS recorder were used to record behavior, which was later analyzed in slow motion. Vouchers of all insect species are deposited in the Instituto Nacional de Biodiversidad de Costa Rica, Santo Domingo,

Costa Rica, and spiders are deposited in the Museum of Comparative Zoology, Cambridge, Mass.

Obtaining identifications of the specimens was difficult, because of the current lack of arthropod taxonomists. Nearly all identifications were made by specialists. Exceptions that were identified using keys included the bibionid (Hardy 1981), the sciarid (Steffan 1981), and the mantid (Ortega and Marquez 1988). The eumastacid was identified using a voucher collection identified by C. Rowell. Six species that were included in the calculations of frequencies in the results selection are omitted from the Appendix because of lack of identifications. All tests of statistical significance used two-tailed  $\chi^2$  tests.

## RESULTS

The results are summarized in the Appendix. The behavior of five species (four indicated in the Appendix by "?," plus an unidentified sepsid fly) was not easy to interpret (see footnotes 41, 59, 132, 150). These species are all counted as not performing copulatory courtship in the analyses that follow.

On a species-by-species basis, males of 81% of the 131 species showed clear copulatory courtship. Because some species were closely related to others in the survey, however, a phylogenetic bias could be present in either male behavior or in female selectivity. This is because the behavior of some groups of species might be the result of acquisition of such behavior in a common ancestor and its subsequent conservation in descendants without favorable selection. If this has occurred, the behavior should be counted in a survey like this only once for all species descended from each common ancestor in which the behavior arose independently (Ridley 1983; Felsenstein 1985). Similar high frequencies of occurrence were obtained, however, when the data were analyzed by higher groupings: the frequency of copulatory courtship was 79% for 102 genera, and 76% for 49 families. All three frequencies are more than twice as high as those from the sample of previously published accounts of the behavior of 302 species in 231 genera in 102 families (Eberhard 1991) (all differences,  $P < 0.001$ ).

In fact, observations of congeneric species indicate that phylogenetic bias is unlikely, at least with respect to male copulatory courtship behavior. If one uses conservative comparisons (considering only the presence/absence of differ-

ent types of behavior without considering possible differences in sequences, timing, and duration), there were intrageneric differences in all 17 genera: seven species of the chafer beetles *Phyllophaga*; four species of the spiders *Leucauge* and the soldier beetles *Chauliognathus*; three species each of the assassin bugs *Apiomerus*, the pentatomid bugs *Mormidea*, the stainer bugs *Dysdercus*, and the weevils *Lixus*; and two species each of the scarab beetles *Strigoderma*, the plant beetles *Calligrapha*, the flea beetles *Brachypnoea*, the tortoise beetles *Omaspides*, the ladybird beetles *Epilachna*, the tiger beetles *Pseudoxychila*, the weevils *Macromerus*, the lygaeid bugs *Xyonysius*, the flies *Richardia*, and the soldier flies *Merosargus*. Previous studies of other species in the same genera as species of this study allow comparisons in three more genera, and all show intrageneric differences: two species of the ephydrid flies *Ochthera* (Simpson 1975); four species of the chafer beetles *Macrodactylus* (Eberhard 1993); and three species of the plant beetle *Macrohaltica* (Eberhard and Kariko in prep.).

A similar trend for copulatory courtship to vary intragenerically (61% of 31 genera) was noted in previously published accounts (Eberhard 1991). The data presented here, however, are more convincing. In previous studies, the differences in 37% of the genera that showed interspecific variation included cases in which one species apparently lacked copulatory courtship, possibly an artifact of incomplete reporting of copulation behavior (Eberhard 1991; see Discussion). Copulatory courtship was lacking in only 3 of the 56 species compared intragenerically in the present study.

In fact, *intraspecific* differences in copulatory courtship were found in the pentatomid bug *Mormidea notulata* and the weevil *Nicentrus lineicollis* (L. H. Rolston and C. Lyell kindly checked the respective specimens from Colombia, Panama, and Costa Rica, and found no distinguishing morphological differences). Geographic variation in copulatory courtship also occurs in the halictid bee *Nomia triangulifer* (Wcislo et al. 1992). Intrageneric and intraspecific variation suggest rapid divergent evolution relative to other characters, indicating that copulatory courtship in a given group is not often likely to be explained as a relatively invariable plesiomorphic trait inherited without selection from some common ancestor. Thus, corrections for the possibility of phylogenetic bias of the sort

discussed by Ridley (1983) and Felsenstein (1985) are not included in the analyses that follow.

The related but distinct question of a phylogenetic bias with respect to female discriminatory processes that would favor the evolution of male copulatory courtship cannot be answered definitively without further observations of other groups. In mammals, the best-studied major group other than insects with respect to copulation behavior, males often perform behavior during copulation that apparently represents courtship (Dixon 1987; Dewsbury 1988).

## DISCUSSION

### A. Biases in Previous Studies

The data of this study suggest that previous studies have been biased against reporting copulatory courtship. The overall frequency of copulatory courtship was more than double that of previous studies (81% versus 36%). Fewer species lacked copulatory courtship in intrageneric comparisons (6% versus 37%). In two cases (the staphylinid *Leistotrophus versicolor* and the bruchid *Zabrotes subfasciatus*), a previous account (Forsythe and Alcock 1990; Singh et al. 1979) failed to mention male copulatory courtship behavior (it is possible that behavioral differences between populations of these species might account for the differences in observations).

Another indication of previous biases is that the proportion of the behavior patterns in copulatory courtship that did not also occur before intromission was also higher in this study (65% of 125 patterns versus 56% of 147 in the literature sample), although in this case the difference is not statistically significant ( $P > 0.1$ ,  $\chi^2 = 2.22$ ,  $df = 1$ ). A further indication is the greater number of different types of copulatory courtship behavior seen in each species in which it occurred. More than one behavior pattern was noted in 56% of the 106 species with copulatory courtship, as compared with 36% of the 109 species in the sample of previous studies (Eberhard 1991) ( $P < 0.001$ ,  $\chi^2 = 9.03$ ,  $df = 1$ ).

Finally, genitalic movements by the male were noted in 63% of the 107 species observed in sufficient detail in this study, whereas this behavior was mentioned in only 5% of the 302 species in the literature sample ( $P \ll 0.001$ ,  $\chi^2 = 191$ ,  $df = 1$ ).

The higher frequency of male copulatory courtship found here is perhaps not surprising. Detailed observations revealed some relatively cryptic courtship behavior, such as the repeated

but infrequent bouts of tapping movements of otherwise immobile *Apiomerus* males (as little as about 1 s of movement every 10–15 min during a several-hour copulation), and the small amplitude but sustained vibrating or rocking movements of *Chauliognathus* soldier beetles, *Stenomacra* bugs, and *Prosapia* spittle bugs, which would have been all but imperceptible in the swaying vegetation of their natural environments. The higher rates reported here thus may be closer to the “true” values. Presumably the underreporting of copulatory courtship in previous studies was caused, at least in part, by previous lack of a theoretical framework (such as cryptic female choice) in which such behavior made sense.

Having said this, I hasten to report some counterintuitive observations of my own. In six species (the pyrrhocorid bug *Dysdercus mimulus*, the lygaeid bug *Ozophora pallescens*, the largid bug *Largus* sp., the pentatomid bug *Mormidea* sp., the philopotamid caddisfly *Chimarra* sp., and the rhipipterygid orthopteran *Rhipipteryx biolleyi*), females performed behavior during copulation that clearly met the criteria for courtship behavior (prolonged body shaking, rubbing or tapping the male with her hind legs, or persistent, rhythmic swinging of her body). In several others (e.g., the soldier beetles *Chauliognathus*, the tiger beetles *Pseudoxychila*, the flies *Richardia*), the female repeatedly pushed the male with her legs in apparent attempts to uncouple. Perhaps some males use their genitalia to manipulate females or the sperm stored inside them in some way that can be disadvantageous for the female. Or perhaps females were attempting to cause males to desist before they transferred sperm, free themselves more rapidly from coupling, or induce the male to deposit more sperm or accessory products that are useful to the female nutritionally, or to provide a wider array of sperm and thus perhaps a better chance of obtaining high-quality offspring (Watson 1991).

### B. Biases in This Study

There are several reasons to believe that the data reported here represent underestimates of the frequency of male copulatory courtship in these species. Some samples are relatively small; thus, infrequent copulatory courtship behavior may have been missed. Of the 27 species that were observed only once, 48% did not perform copulatory courtship (including both N and “?” in the Appendix plus two additional species)

(compared with 19% in the entire sample, the difference is significant,  $P < 0.001$ ,  $\chi^2 = 18.3$ ,  $df = 1$ ). In addition, some “copulations” may have in fact been internal rejections of the male genitalia by the female, as apparently occurs in some (Eberhard 1993; Eberhard and Kariko in prep.), and may have thus been terminated prematurely. I also did not check mating pairs for odors (and would presumably have failed in any case to sense many pheromones) or for substrate vibrations (in the bug *D. mimulus* the male apparently spread a liquid on the outer surface of the female’s abdomen during copulation; see footnote 115 in the Appendix).

Use of species-specific structures to hold or clasp the female (e.g., the spiders *Tetragnatha* sp., *Leucauge* spp., and *Physocyclus globosus*, possibly the tiger beetles *Pseudoxychilus* spp., the chafer beetles *Strigoderma* spp.) was also not counted, although studies of some groups (e.g., odonates, Robertson and Paterson 1982; anacostracan crustaceans, Belk 1984) have shown that clasping organs of this sort can induce female responses that are crucial for reproduction. One of the cues used to recognize courtship behavior was rhythmic repetition (see Materials and Methods); thus, nonrhythmic courtship movements would have gone uncounted (e.g., intermittent, isolated abdominal movements of one *Chauliognathus* soldier beetle were not counted, although similar movements that were highly rhythmic and sustained in two other species were counted).

In addition, rhythmic thrusting, twisting, or contracting movements of the male genitalia occurred in at least 63% of the 107 species in which this detail was checked. In 11 of the 25 species counted as lacking copulatory courtship, male genitalia moved rhythmically during copulation (the overall frequency of copulatory courtship would be 89% if rhythmic genitalic movements were counted as courtship). Rhythmic genitalic movements have been demonstrated to induce the female to discard sperm from previous males in the tettigoniid *M. ornatus* (von Helversen and von Helversen 1991). An alternative function, direct sperm removal, is also possible.

Also not counted were multiple intromissions (five additional species in which neither copulatory courtship nor other genitalic movements were seen), even though these behavior patterns may again function as courtship (Eberhard 1985; Dewsbury 1988; Watson 1991). The fact that genitalic thrusting or pushing patterns in the bee-

tles *Macrohaltica* vary intragenerically (Eberhard and Kariko in prep.; footnote 40 in the Appendix) is in agreement with the idea that this behavior is under sexual selection.

Finally, "cryptic" genitalic thrusting also occurred in five other species in which the female's transparent body wall allowed me to see that an apparently immobile male was moving his genitalia rhythmically inside the female. Cryptic internal thrusting movements also occur in some cassidine beetles (D. Windsor, V. Rodriguez unpubl. data). The rhythmic back and forth flow of material seen through the transparent walls of the male genitalia of some other species in this study (e.g., the spittle bugs *Zulia* sp., many of the beetles—see footnotes 13, 27, 29, 31, 38, 75, 84, 86, 100, 107, 121 in the Appendix) may have been associated with such cryptic internal thrusting movements. Similar movements may occur in species in which genitalia and body walls are not transparent.

In sum, it is probable that the data presented here underestimate the true frequency of copulatory courtship in the species studied. The question remains of whether these species constitute a representative sample of insects and spiders. Obviously the sample, which was determined largely by ease of study (see Materials and Methods), is biased taxonomically toward Coleoptera, Hemiptera, Diptera, and araneoid spiders. Within Coleoptera, Chrysomelidae and Curculionidae were most often studied. I know of no a priori reason to suppose that any of these taxa are atypical with respect to copulatory courtship. Further studies are needed in other groups, such as Lepidoptera, in which published accounts seldom mention copulatory courtship (Eberhard 1991).

There is reason to suspect that this sample (and for that matter, the entire published literature on copulation behavior) probably does have a bias, which favors those species in which females often remate. In species in which females remate less often, a female would be less likely to accede to a male's precopulatory courtship while an observer watched. Some species I attempted to observe did not copulate and are thus not included in the results; in some of these, females consistently rejected courting males.

A bias toward multiple mating in females should favor inclusion of species in which cryptic female choice is more likely to occur because cryptic female choice between males is possible only if females sometimes mate more than once, and its effects on male fitness are likely to be

larger when females mate with more males. The frequency of multiple mating by females in nature is still an open question for most species (Eberhard 1985). Judging by the few groups in which minimum estimates of female remating frequencies in the field have been documented from vestiges left by males that have succeeded in transferring material to the female (e.g., spermatophores in butterflies, Ehrlich and Ehrlich 1978), and from genetic analyses of the offspring of single females in birds (Westneat et al. 1990; Birkhead and Møller 1992), multiple mating seems much more common than single mating.

An additional bias toward copulatory courtship may have been introduced when some species were chosen for study because they were in genera in which I had already studied other species. When the 22 species that were chosen for this reason are subtracted (some additional species with congeners in this study were chosen because of ease of observation, in ignorance that they were congeners of species already studied), the overall frequency of copulatory courtship slips from 81% to 77%.

In sum, there are probably conflicting biases affecting the measured frequency of copulatory courtship. The data presented here probably underestimate the frequency of copulatory courtship *within* the sample. The sample itself may be biased to give an overestimate of the frequency of copulatory courtship in these groups in general. The relative sizes of these biases are unknown.

Sperm or spermatophores containing sperm emerged from the female during or just following copulation in at least 25% of 53 species observed with sufficient care. This frequency of sperm emission contrasts sharply with 0 of 302 species in the sample of previously published accounts (Eberhard 1991) ( $P < 0.001$ ,  $\chi^2 = 74$ ,  $df = 1$ ) and suggests that sperm emission may be more common than previously appreciated. It has been noted recently in the fly *Dryomyza anilis* (Otrotnen and Siva-Jothy 1991), the tettigoniid *M. ornatus* (von Helversen and von Helversen 1991), and some cassidine beetles (D. Windsor and V. Rodriguez in prep.). The data presented here again may represent serious underestimates. Sperm emission that did not occur either during or very soon after copulation would have been missed. In addition, I did not check for sperm clinging to the male's genitalia when they were withdrawn [as occurs in odonates (Waage 1983; for exceptions, see footnotes 64 and 66 in the Appendix)].

Whether the sperm I observed emerging belonged to the copulating male or to previous males, and whether it was removed by the male or by the female remains to be established in the species studied here. In both *D. anilis* and *M. ornatus*, it belongs to previous males and is discarded by the female rather than being directly removed by the male (Otronen and Siva-Jothy 1991; von Helversen and von Helversen 1991).

### *C. Possible Function and Significance of Copulatory Courtship*

It is possible that some males court during copulation to induce the female to accede to additional intromission attempts. In a large majority (81%) of the 94 species with copulatory courtship in which postcopulatory behavior was observed, however, the male left the female as soon as copulation ended (includes all those species in which males left immediately after copulation in at least some pairs). In nearly all cases, the male left without overt rejection behavior by the female. Males of species in which copulatory courtship did not occur left females with a similar frequency (85% of 20 species). Thus, copulatory courtship probably generally does not function to induce the female to accept further copulation attempts by the male.

A second possibility is that copulatory courtship serves to inform the female of the male's species identity. If this were true, one would expect copulatory courtship to be especially common in those species in which no precopulatory courtship occurs. The predicted trend was weak and insignificant, however; 73% of 71 species with precopulatory courtship also had copulatory courtship, as compared with 84% of 20 species without precopulatory courtship ( $0.5 > P > 0.2$ ,  $\chi^2 = 1.14$ ,  $df = 1$ ).

Although these functions are not ruled out for all species, they nevertheless seem not to be general explanations. The behavior patterns observed, which included rhythmic licking, biting, tapping, rubbing, jerking, scraping, shaking, rocking, lifting, pressing, twisting, jabbing, and squeezing the female as well as waving and singing to her, need explanation. In no case did this behavior involve either direct manipulation or removal of sperm from previous males, or forcing the female to execute any other reproductive function; nor was it directed in any sense toward other males (absent in most cases). Thus, the courtship behavior could not achieve its presumed male fitness-enhancing functions directly

but only through induction of responses by females. Taking into account the arguments in the introduction and the criteria used to discriminate courtship behavior (Materials and Methods), the most likely general function of copulatory courtship is thus to elicit female responses during or following copulation that increase the male's chances of fathering her offspring.

In a few cases, copulatory courtship may represent attempts to induce the female to remain still, because male behavior seemed elicited by the initiation of movements by the female. In most species, however, the context of the behavior did not suggest this function, and other possibilities (permit deeper penetration, allow sperm transfer, transport sperm to storage sites, refrain from discarding it, refrain from remating with subsequent males, and so on) seem more likely.

If copulatory courtship is even nearly as widespread as this study suggests, and if, as just argued, it often functions to influence cryptic female choice, there are several important consequences for the study of sexual selection. The reproductive success of males cannot necessarily be measured by simply counting numbers of copulations or females mated. As Thornhill has written, "Although some relationship between male fitness and mating success exists, it is probably rarely . . . simple" (Thornhill 1983, p. 785), and more direct data on paternity are necessary. Studies of male courtship behavior should also routinely include observations of the male's behavior during copulation.

Many of the copulatory courtship behavior patterns documented here seem poorly designed to give the female information regarding the overall vigor of the male. Thus, this study lends support to the idea that sexual selection by female choice often may focus instead on males' abilities to emit signals (see also Eberhard 1993a). This study also reinforces doubts regarding Darwin's idea that some male structures such as genitalia and clasping devices that are brought into play only after copulation has begun are not under sexual selection (Darwin 1871). These structures, like the male's copulatory courtship behavior, may often be subject of cryptic female choice (Eberhard 1985).

### ACKNOWLEDGMENTS

I thank the students of the "Copulas" course, V. Rodriguez, R. L. Rodriguez, M. C. Marin, C. Marquez, S. Lobo, and L. Diaz, for stimulating

discussions and for kindly allowing me to use their unpublished data. I also thank the Centro de Ecología of the Universidad Nacional Autónoma de México, and the Fundación para Educación Superior in Colombia for invitations that resulted in some of the observations reported here. I owe a debt of gratitude to the small army of people who kindly took time to identify specimens for me: G. Arango (cercopids); H. Brai-lovsky (reduviids); J. Chapin (coccinellids); C. Deeleman-Reinhold (pholcids); J. Doyen (tenebrionids); C. Godoy (clastopterids); E. Fisher (asilids); W. Flowers (chrysomelids); R. Freitag (cicindellids); D. Furth (chrysomelids); R. Gordon (cantharids, coccinellids); D. Grimaldi (drosophilids, richardiids); P. Hanson (scelionids); T. Henry (lygaeids, pyrrhocorids, reduviids, saldids); H. Hespenheide (buprestids); H. Howden (scarabs); J. Kingsolver (bruchids); H. W. Levi (theridiids, tetragnathids); H. Lezama (cerambycids); C. Lyell (carabids, corylophids, curculionids, scaphidiids); M. A. Morón (scarabs); F. Muñoz (philopotamids); D. Nickle (rhipipterygids); A. L. Norrbom (sepsids, richardiids, nereids, micropezids, tephritids); R. Packauskas (coreids); J. Pakaluk (curculionids, languriids, erotylids); A. Pont (muscid); L. H. Rolston (pentatomids); C. Schaefer (pentatomids, largids, pyrrhocorids); J. Slater (lygaeids); A. Solis (scarabs, cantharids, zopherids); H. Stockwell (curculionids); C. Thompson (fly families); E. Wiley (cassidines); D. Windsor (chrysomelids); D. Wittmer (cantharids); and N. E. Woodley (stratiomyids). I also thank D. Clark, A. Fernandez, A. Miranda, and C. Valderrama, who provided specimens, M. Lacey-Theisen, who helped coordinate identification efforts, and W. Wcislo and M. J. West-Eberhard, who commented on a draft of the manuscript.

## LITERATURE CITED

- Alcock, J., and S. Buchmann. 1985. The significance of post-insemination display by male *Centris pallida* (Hymenoptera: Anthophoridae). *Zeitschrift fuer Tierpsychologie* 68:231-243.
- Assem, J. van den, and J. Visser. 1976. Aspects of sexual receptivity in the female *Nasonia vitripennis* (Hymenoptera: Pteromalidae). *Biology of Behavior* 1:37-56.
- Bateson, P. 1983. *Mate choice*. Cambridge University Press, Cambridge.
- Belk, D. 1984. Antennal appendages and reproductive success in the *Anostraca*. *Journal of Crustacean Biology* 4:66-71.
- Birkhead, T., and F. Hunter. 1990. Mechanisms of sperm competition. *Trends in Ecology and Evolution* 5:48-52.
- Birkhead, T., and A. P. Møller. 1992. *Sperm competition in birds*. Academic Press, New York.
- Bradbury, J., and M. Andersson. 1987. *Sexual selection: testing the alternatives*. Wiley, New York.
- Crews, D. 1987. Courtship in unisexual lizards: a model for brain evolution. *Scientific American* 257(6):72-77.
- Darwin, C. 1871. *The descent of man and selection in relation to sex* (reprinted). Random House, New York.
- Dewsbury, D. 1988. Copulatory behavior as courtship communication. *Ethology* 79:218-234.
- Dixon, A. F. 1987. Observations on the evolution of genitalia and copulatory behavior in primates. *Journal of Zoology* 213:423-443.
- Eberhard, W. G. 1985. *Sexual selection and animal genitalia*. Harvard University Press, Cambridge.
- . 1990. Animal genitalia and female choice. *American Scientist* 78:134-141.
- . 1991. Copulatory courtship and cryptic female choice in insects. *Biological Reviews of the Cambridge Philosophical Society* 66:1-31.
- . 1992. Species isolation, genital mechanics, and the evolution of species-specific genitalia in three species of *Macrodactylus* beetles (Coleoptera, Scarabeidae, Melolonthinae). *Evolution* 46:1774-1783.
- . 1993b. Copulatory courtship and genital mechanics of three species of *Macrodactylus* (Coleoptera, Scarabeidae, Melolonthinae). *Ecology, Ethology and Evolution* 5:19-63.
- . 1993a. Evaluating models of sexual selection: genitalia as a test case. *American Naturalist* 142:564-571.
- . 1993c. Copulatory courtship and the morphology of genitalic coupling in seven *Phyllophaga* species (Coleoptera, Melolonthidae). *Journal of Natural History* 27:683-717.
- Ehrlich, A., and P. Ehrlich. 1978. Reproductive strategies in the butterflies. I: Mating frequency, plugging, and egg number. *Journal of the Kansas Entomological Society* 51:666-697.
- Felsenstein, J. 1985. Phylogenies and the comparative method. *American Naturalist* 125:1-15.
- Forsythe, A., and J. Alcock. 1990. Female mimicry and resource defense polygyny by males of a tropical rove beetle, *Leistotrophus versicolor* (Coleoptera: Staphylinidae). *Behavioral Ecology and Sociobiology* 26:325-330.
- Hardy, D. E. 1981. Bibionidae. Pp. 217-222 in J. F. McAlpine et al., eds. *Manual of Nearctic Diptera*. Research Branch Agriculture Canada, Monograph 27, Ottawa, Canada.
- von Helversen, D., and O. von Helversen. 1991. Premating sperm removal in the bushcricket *Metaplastes ornatus* Ramme 1931 (Orthoptera, Tettigoniidae, Phaneropteridae). *Behavioral Ecology and Sociobiology* 28:391-396.
- Immelmann, K., and C. Beer. 1989. *A dictionary of ethology*. Harvard University Press, Cambridge.
- Morón, M. A. 1986. *El Genero Phyllophaga en Mexico*. Instituto de Ecología, Publication 20, Mexico.
- Ortega, G., and M. Marquez. 1988. Orthopteros de la estación de biología "Chamela," Jalisco (Insecta;

- Orthoptera). *Anales del Instituto de Biología de la Universidad Nacional Autónoma de México*, 58 Serie de Zoología (1):35–62.
- Otronen, M., and M. Siva-Jothy. 1991. The effect of postcopulatory male behavior on ejaculate distribution within the female sperm storage organs of the fly *Dryomyza anilis* (Diptera: Dryomyzidae). *Behavioral Ecology and Sociobiology* 29:33–37.
- Palmer, M. 1976. Natural history and behavior of *Pseudoxychila tarsalis* Bates. *Cicindela* 8:61.
- Ridley, M. 1983. The explanation of organic diversity. The comparative method and adaptations of mating. Oxford Press, Clarendon.
- Robertson, H. M., and H. E. H. Paterson. 1982. Mate recognition and mechanical isolation in *Enallagma* damselflies (Odonata: Coenagrionidae). *Evolution* 36:243–250.
- Rodriguez, V. 1994a. Mating behavior in *Charidotella* sp. nr. *sexpunctata* (Coleoptera: Chrysomelidae: Cassidinae). *Coleopterists Bulletin*.
- . 1994b. Sexual behavior in *Omaspides convexicollis* and *Omaspides bistrata* (Coleoptera: Chrysomelidae: Cassidinae) with notes on maternal care of eggs and young. *Coleopterists Bulletin*.
- Simpson, K. W. 1975. Biology and immature stages of three species of nearctic *Ochthera* (Diptera: Ephydriidae). *Proceedings of the Entomological Society of Washington* 77:129–155.
- Singh, T., K. Inderjeet, and M. S. Saini. 1979. Biology of *Zabrotes subfasciatus* (Boh.) (Bruchidae: Coleoptera). *Entomon* 4:201–203.
- Sivinski, J., T. Burk, and J. C. Webb. 1984. Acoustic courtship signals in the Caribbean fruit fly, *Anastrepha suspensa* (Loew). *Animal Behavior* 32:1011–1016.
- Steffan, W. A. 1981. Sciaridae. Pp. 247–255 in J. F. McAlpine et al., eds. *Manual of Nearctic Diptera*. Research Branch Agriculture Canada, Monograph 17, Ottawa, Canada.
- Thornhill, R. 1983. Cryptic female choice and its implications in the scorpionfly *Harpovittacus nigriceps*. *American Naturalist* 122:765–788.
- Waage, J. K. 1983. Sperm competition and the evolution of odonate mating systems. Pp. 251–290 in R. L. Smith, ed. *Sperm competition and the evolution of animal mating systems*. Academic Press, New York.
- Watson, P. J. 1991. Multiple paternity as bet-hedging in female sierra dome spiders, *Linyphia litigiosa* (Linyphiidae). *Animal Behavior* 41:343–360.
- Weislo, W. T., R. L. Minkley, and H. Spangler. 1992. Precopulatory courtship behavior in a solitary sweat bee *Nomia triangulifera* (Hymenoptera: Halictidae). *Apidologie* 23:431–442.
- Westneat, D. F., P. W. Sherman, and M. L. Morton. 1990. The ecology and evolution of extra-pair copulations in birds. *Current Ornithology* 7:331–369.

Corresponding Editor: G. Vermeij



APPENDIX Continued.

Taxon	Site of observation <sup>1</sup>	N <sup>2</sup>	Male copulatory courtship behavior pattern <sup>3</sup>	Male mounted after copulation?	Sperm emerge? <sup>4</sup>	Pre-copulatory courtship?	Copulation court same as precopulation?	Genital events	Reference <sup>5</sup>
<i>Brachynoea</i> sp.	FM	0, 2	legs II tap, rub elytra <sup>25</sup> antennae vibrate	?	?	?	?	?	
<i>Calligrapha</i> cf. <i>fulvipes</i> Stal	CM	2, 4	mandibles rub/bite elytra <sup>22,26</sup> body rocks laterally <sup>27</sup>	Y/N	Y	Y	N	two types of thrusts <sup>27</sup>	
<i>Calligrapha</i> sp.	CMV	0, 3	legs I and II tap elytra	Y	Y <sup>28</sup>	?	N	rhythmic thrusts <sup>29</sup>	
<i>Calceophana</i> sp.	CM	0, 2	antennae tap prothorax <sup>30</sup>	Y	?	?	?	two types of thrusts <sup>31</sup>	
<i>Chalepus</i> sp.	CM	1, 0	no movement <sup>32</sup>	N	?	N	N	no movement <sup>33</sup>	CM
<i>Charidotella</i> sp. nr. <i>sexpunctata</i>	CMV	11, 0	legs III strike elytra stridulate with head	N	Y	N	N	rhythmic in-out movement of material inside	VR
<i>Colaspis sanjoseana</i>	CM	0, 6	raise female body rhythmically mandibles rub elytra <sup>34</sup> legs III rub venter	N	N	Y?	Y	male genitalia two types of thrusts <sup>31</sup>	
<i>Lema</i> sp.	CM	0, 1	body vibrates <sup>35</sup> stridulate <sup>36</sup>	N	?	?	?	rhythmic thrusts <sup>31</sup>	
<i>Lepinotarsa undecimlineata</i>	CM	14, 0	mouthparts touch femur II	Y <sup>37</sup>	N	N	N	rhythmic thrusts <sup>38</sup>	
<i>Macrohhalica</i> sp.	CM	1, 1	mandibles scrape elytra	Y	?	Y	N	rhythmic thrusts <sup>40</sup>	
<i>Mastostethus nigricinctus</i> Chevrolat	CM	1, 0	tarsi III rub abdomen <sup>39</sup> <sup>41</sup>	N	?	N?	N	rhythmic movements <sup>42</sup>	
<i>Megalotopus armatus</i> Lacordaire	CMV	7, 2	body jerks, stridulates mouthparts rub pronotum with complex movements	N <sup>43</sup>	N	Y	Y	rhythmic thrusts	MCM
<i>Omaspides bistriata</i>	CMV	8, 4	lean dorsally and tarsi I rub elytra	N	N	N	N	rhythmic thrusts	VR
<i>Omaspides convexicollis</i>	CMV	5, 3	legs II and III strike elytra mouthparts tap dorsum	N	N	N	N	rhythmic thrusts	VR
<i>Plagiometriona calavata</i> (Fab.)	CM	1, 0	head vibrates side-to-side <sup>8,44</sup> body shudders and tarsi I tap elytra <sup>8,45</sup>	N	?	Y	N	rhythmic in-out movement of material inside male genitalia	
<i>Platyphora ligata</i> (Stal)	CMV	4, 0	head vibrates <sup>8</sup> body vibrates rapidly side-to-side <sup>46</sup> mandibles scrape elytra <sup>22,48</sup>	Y	Y <sup>17,46</sup>	N <sup>47</sup>	Y	short, rapid thrusts	
<i>Systema chloropus</i> Harold	F	0, 1	legs I, II rub elytra <sup>49</sup> legs III rub abdomen	N	?	?	?	?	
<i>Varicoxa</i> sp.	CM	0, 3	antennae, legs II rub sides <sup>50</sup>	?	?	?	?	rhythmic thrusting <sup>51</sup>	
Cicindellidae	F	1, 10	vibrates entire body <sup>8</sup> antennae tap antennae	?	?	?	?	?	
<i>Oxycheila carthagera</i> Dejean	CMV	4, 0	legs I hit antennae body shudders	Y/N	?	?	N	in-out movement early in copulation	
<i>Oxycheila polita</i> Banks	CMV	4, 0	body shudders	Y/N	?	?	N	four types of thrust	RLR, WE
<i>Pseudoxychila bipustulata</i>	FCM	31, 0	legs II rub elytra <sup>17,52</sup>	Y/N	Y	N <sup>52</sup>	N		

APPENDIX Continued.

Taxon	Site of observation <sup>1</sup>	N <sup>2</sup>	Male copulatory behavior pattern <sup>3</sup>	Male mounted copulation?	Sperm emerge? <sup>4</sup>	Pre-copulatory courtship?	Copulation court same as precopulation?	Genitalia events	Reference <sup>5</sup>
<b>Latreille</b>									
<i>Pseudoxychila tarsalis</i> Bates	FCMV	45, 0	legs II rub legs, elytra, abdomen <sup>17,52</sup>	Y/N	Y	N <sup>52</sup>	Y	four types of thrust	RLR, WE
<b>Coccinellidae</b>									
<i>Cycloneda sanguinea</i> (L.)	CM	2, 8	legs III rub pygidium	Y <sup>17</sup>	N	N	N	mvt. tip of abdomen <sup>53</sup>	SL
<i>Brachiacantha lepida</i> Mulsant	CM	5, 6	legs III rub pygidium	N <sup>17</sup>	N	N	N	moving tip of abdomen <sup>53</sup>	SL
<i>Epitachna borealis</i> Guerin	CM	2, 0	legs III vibrate <sup>8</sup>	N	?	N <sup>54</sup>	?	?	
			genitalia process taps sternite <sup>55</sup>						
			mouthparts rub/tap elytra <sup>54</sup>						
<i>Epitachna vineta</i> Crotch	CM	5, 0	legs III rub/tap rear margin, elytra <sup>56</sup>	Y/N	?	N <sup>57</sup>	Y	no movement <sup>58</sup>	
<b>Corylophidae</b>									
<i>Orthopterus</i> sp.	CMV	3, 9	? <sup>59</sup>	N	?	? <sup>59</sup>	Y	thrusts (speed, depth vary)	
<b>Curculionidae</b>									
<i>Cleistolophus similis</i> Chevrolat	CM	0, 2	legs III rub abdomen <sup>60</sup> body jerks with mouthparts on elytra	Y/N	?	Y	N	rhythmic movements of abdomen <sup>61</sup>	
			stridulate						
			rostrum scrapes dorsum	Y	N	Y	N	rhythmic movements of abdomen <sup>61</sup>	VR
			stridulate <sup>62</sup>						
<i>Cleogonus</i> sp. nr. <i>rubetra</i> (Fab.)	CMSV	7, 1	body rocks sharply rearward <sup>63</sup>	Y	N <sup>64</sup>	Y	?	complex rhythmic movements <sup>61</sup>	
<i>Lixus cavicollis</i> Champion	CM	0, 2	rostrum taps head <sup>65</sup>	Y	N <sup>66</sup>	?	?	complex rhythmic movements <sup>61</sup>	
<i>Lixus</i> sp.	CM	0, 1	head vibrates rapidly laterally <sup>8</sup>	Y/N	Y <sup>28</sup>	?	?	complex rhythmic movements <sup>61</sup>	
<i>Lixus</i> sp.	CM	0, 2	no movement	Y	?	?	?	rhythmic movements of abdomen	
<i>Macromerus bicinctatus</i>	F	2, 0	stridulate <sup>22,67</sup>	N	N	Y	Y	rhythmic movements of abdomen	
<i>Macromerus</i> sp.	CMV	6, 0	legs I rub and embrace female <sup>68</sup>	Y/N	N	Y	Y	rhythmic movements of abdomen	
<i>Metamasius</i> sp.	CM	2, 3	mouthparts rub pronotum				?		
<i>Nicentrus lineicollis</i> Boh. (Panama)	CMV	0, 8	rostrum, mandibles wiped on prothorax	Y	? <sup>70</sup>	Y	Y <sup>71</sup>	rhythmic movements of abdomen <sup>61</sup>	
(Costa Rica)	CM	1, 5	body shudders <sup>69</sup> rostrum wipes prothorax	Y	?	Y	N	rhythmic movements of abdomen <sup>72</sup>	
			legs III vibrate				Y		
			legs II, III rub abdomen <sup>73</sup>				N		
<i>Pantoloides</i> sp.	CM	3, 9	no movement	Y/N	N	Y	-	no movement	SL
<i>Peridinetus irroratus?</i> (Fab.)	CMV	1, 3	legs I wave <sup>74</sup>	N	N	Y	Y	rhythmic movements of abdomen <sup>75</sup>	

APPENDIX Continued.

Taxon	Site of observation <sup>1</sup>	N <sup>2</sup>	Male copulatory behavior pattern <sup>3</sup>	Male mounted after copulation?	Sperm emerge <sup>4</sup>	Pre-copulatory courtship?	Copulation court same as precopulation?	Genital events	Reference <sup>5</sup>
<i>Rhinospatha albomarginalia</i> Ch.	CMV	1, 23	no movement <sup>6</sup>	Y	Y <sup>77</sup>	Y	—	movements of abdomen <sup>61,76</sup>	LD
<i>Rhodobaenus plicatus</i> Champ.	CV	1, 0	legs I tap sides thorax and femora of legs II	N	?	?	?	?	VR
Erotyliidae									
<i>Homoeotelus</i> sp.	CM	1, 0	legs III rub elytra <sup>78</sup>	N	?	Y <sup>79</sup>	N	rhythmic movements <sup>12</sup>	VR
<i>Mycotretus</i> sp.	CMV	36, 0	head thorax move rhythmically <sup>44</sup> mouthparts tap pronotum <sup>22</sup>	Y	N	N	N	rhythmic movements	VR
<i>Triplax</i> sp.	CMV	4, 10	head, thorax move rhythmically <sup>44</sup> legs III rub elytra	?	N	Y	N	rhythmic movements	VR
Languriidae									
<i>Hapalips suturalis</i> Champion	CM	2, 1	mouthparts tap pronotum <sup>80</sup>	N	?	Y	Y	rhythmic thrusts <sup>81</sup>	
Melonthiidae									
<i>Astaena</i> sp.	F	0, 2	body rocks side-to-side <sup>82</sup>	?	?	?	?	?	
<i>Macrodaclylus</i> sp.	CM	0, 7	head vibrates with antennae on eyes or pronotum <sup>83</sup> legs II vibrate legs III vibrate	Y	?	Y	Y	rhythmic thrusts	
<i>Phyllophaga aequata</i>	FCM	0, 3	legs II hit antennae	N	?	?	?	cryptic thrusts <sup>84</sup>	WE
<i>Phyllophaga</i> sp. nr. <i>anodenitata</i>	F	0, 3	body waggles side-to-side legs II rub abdomen legs II vibrate in air <sup>8</sup>	?	N	?	?	no movement	WE
<i>Phyllophaga obsoleta</i>	F	0, 2	abdominal sternite rubs pygidium <sup>85</sup> tarsi I rub elytra, pygidium	?	?	?	?	cryptic thrusts <sup>84</sup>	WE
<i>Phyllophaga setidorsis</i>	FCM	0, 5	abdominal sternite rubs pygidium <sup>85</sup>	N	N	Y	?	cryptic thrusts <sup>84</sup>	WE
<i>Phyllophaga setifera</i> var. <i>menetresii</i> (Blanch)	FV	0, 6	abdominal sternite rubs pygidium <sup>85</sup> no movement	N	N	Y	—	no movement <sup>86</sup>	WE
<i>Phyllophaga valeriana</i>	FCMV	0, 28	tarsi I rub elytra, pygidium abdominal sternite rubs pygidium <sup>85</sup>	?	?	?	?	no movement	WE
<i>Phyllophaga vicina</i>	FCMV	0, 14	tarsi I rub elytra	N	N	Y	N	cryptic thrusts <sup>84</sup>	WE
<i>Strigoderma intermedia</i> Bates	CM	2, 2	abdominal sternite rubs pygidium <sup>85</sup> legs I and/or II rub elytra <sup>87</sup>	Y/N	?	Y	Y	no movement <sup>88</sup>	
<i>Strigoderma vestita</i> Burm.	CMV	0, 10	head vibrates <sup>44</sup> legs III vibrate <sup>89</sup>	Y	?	Y	Y	no movement	
Scaphidiidae									
<i>Scaphidopsis cf. mexicana</i> Castelnau	CM	1, 2	genital sclerites rub abdomen <sup>90</sup> ventral hairs rub elytra <sup>92</sup> head vibrates <sup>93</sup>	Y/N	Y <sup>91</sup>	Y	N	rhythmic contractions	
Staphylinidae									
<i>Leistrotrophus versicolor</i>	FCMV	11, 0	head vibrates <sup>94</sup>	N	N	Y	Y	some movement <sup>95</sup>	

APPENDIX Continued.

Taxon	Site of observation <sup>1</sup>	N <sup>2</sup>	Male copulatory courtship behavior pattern <sup>3</sup>	Male mounted after copulation?	Sperm emergence? <sup>4</sup>	Pre-copulatory courtship?	Copulation court same as precopulation?	Genitalia events	Reference <sup>5</sup>
<b>Tenebrionidae</b>									
<i>Phaleria gracilipes</i> Casey	CMV	0, 8	legs I, II, III rub elytra mouthparts rub pronotum	N	?	Y	Y	no movement <sup>88</sup>	
<b>Zopheridae</b>									
<i>Zopherus</i> sp.	FH	1, 0	no movement <sup>96</sup>	N	?	Y	—	no movement	
<b>Homoptera</b>									
<b>Cercopidae</b>									
<i>Prosopia bicincta</i> Say	CMV	0, 2	genitalia rub abdomen <sup>97,98</sup> pull rhythmically on female body	N	99	?	N	no movement	
<i>Zulia pubescens</i> (Fab.)	CM	0, 4	genitalia rub base ovipositor <sup>100</sup>	N	Y <sup>101</sup>	Y	N	rhythmic movements <sup>100</sup>	
<b>Clastopteridae</b>									
<i>Clastoptera</i> sp.	CM	0, 1	998,102	N	N	?	?	small rhythmic movements	
<b>Hemiptera</b>									
<b>Coreidae</b>									
<i>Leptoscelis tricolor</i> Westwood	CM	0, 2	tarsi III rub abdomen body shakes side to side <sup>98</sup>	?	?	?	?	no movement	
<i>Spartocera</i> sp. nr. <i>fluca</i> (Thunberg)	CM	1, 2	legs I, II, tap legs, prothorax <sup>103</sup>	Y	?	Y	Y	no movement	
<b>Largidae</b>									
<i>Largus</i> sp.	CMV	0, 2	turn to tap with antennae <sup>98,104</sup> genital capsule vibrates	N	?	?	?	no movement	
<i>Stenomacra marginella</i> (Herrich-Schaeffer)	CMV	0, 3	antennae and proboscis tap head <sup>98,105</sup> genital capsule vibrates head vibrates dorso-ventrally <sup>8</sup>	N	?	Y	Y	sclerite inside male genitalia moves rhythmically	
<b>Lygaeidae</b>									
<i>Neorholomus jamaicensis</i> (Dallas)	CM	1, 2	legs III rub abdomen <sup>106</sup> turn and tap with antennae push	N	N	?	N	several types movement <sup>107</sup>	
<i>Oncopeltus</i> sp.	CM	0, 4	no movement (?) <sup>98,108</sup>	N	N	Y?	Y	no movement	
<i>Ozophora pallescens</i> Distant	CMV	0, 1	vibrate body raised legs III vibrate <sup>8</sup> turn and antennate female <sup>98</sup>	N	?	?	?	no movement	
<i>Xyonyxius</i> sp. nr. <i>basalis</i>	CM	1, 2	legs III push and tap abdomen <sup>109</sup> abdomen vibrates <sup>98</sup>	N	N	Y	?	squeeze female <sup>88,109</sup>	
<i>Xyonyxius californicus</i> (Stal)	CMV	16, 0	genitalia rub abdomen <sup>109</sup> genitalia rub/pinch ovipositor <sup>98</sup>	N	N	Y	N?	no movement	

APPENDIX Continued.

Taxon	Site of observation <sup>1</sup>	N <sup>2</sup>	Male copulatory courtship behavior pattern <sup>3</sup>	Male mounted after copulation?	Sperm emerge <sup>4</sup>	Pre-copulatory courtship?	Copulation court same as precopulation?	Genitalic events	Reference <sup>5</sup>
<b>Pentatomidae</b>									
<i>Acrosternum marginatum</i> (Palisot de Beauvois)	CMV	2, 1	tarsi III tap abdomen <sup>98,110</sup>	N	N	Y	N	no movement	
<i>Mormidea notulata</i> (Herrich-Schaeffer) (Colombia)	CM	0, 3	tarsi III rub/tap abdomen body shudders violently <sup>98,111</sup>	N	?	Y	N	no movement	
(Costa Rica)	CM	0, 10	abdomen vibrates legs III tap abdomen, legs III <sup>98,112</sup>	N	?	Y	Y	no movement	
<i>Mormidea pictiventris</i> Stal.	CM	0, 1	legs III tap and rub legs III, abdomen <sup>98,113</sup>	N	?	?	?	structures inside male genitalia move no movement	
<i>Mormidea</i> sp. n.	CM	0, 7	tarsi III rub female venter <sup>98,114</sup> legs III extended posteriorly <sup>44</sup>	N	?	Y	N	no movement	
<b>Pyrrhocoridae</b>									
<i>Dysdercus mimulus mimulus</i> Hussey	CM	0, 4	legs III tap abdomen <sup>98,115</sup>	N	N	Y	N	rhythmic flexions, pulls	
<i>Dysdercus obliquus</i> Herrich-Schaeffer	CMV	0, 10	no movement <sup>98</sup>	N	?	Y	-	no movement	LD
<i>Dysdercus</i> sp. prob. <i>obscuratus</i> Distant	CMV	0, 10	turn, antennae tap head, legs I, II tap ventral surface <sup>17,98</sup>	N	?	Y	Y	no movement	LD
<b>Reduviidae</b>									
<i>Apiomerus pictipes</i> H.S.	CM	1, 2	legs I, II tap thorax <sup>116</sup> legs I, II twitch <sup>44,118</sup>	N	?	?	N	no movement <sup>117</sup>	
<i>Apiomerus</i> nr. <i>venosus</i>	CM	3, 1	legs I, II tap thorax <sup>116</sup> stridulate <sup>120</sup>	N	?119	Y	N	no movement <sup>117</sup>	
<i>Apiomerus</i> sp.	CMV	0, 3	legs I, II tap thorax <sup>116,121</sup>	Y/N	?	Y	N	no movement <sup>121</sup>	
<i>Poelliopus</i> sp.	CM	4, 3	no movement	Y	?	Y	-	pulsing movement <sup>122</sup>	
Saldidae									
<i>Pentacora</i> sp.	F	0, 4	legs I and II rub female <sup>123</sup>	N	?	N?	N	?	
<b>Diptera</b>									
<b>Asilidae</b>									
<i>Arthopychus pulchellus</i> (Bellardi)	FH	0, 4	wings buzz abdomen twists and jerks female abdomen <sup>98,124</sup>	?	?	?	?	rhythmic contractions	
<b>Bibionidae</b>									
Near <i>Dilophus</i>	FH	0, 2	no movement	N	?	Y	-	rhythmic contractions <sup>125</sup>	
<b>Drosophilidae</b>									
<i>Drosophila</i> sp. n. nr. <i>emarginata</i>	CM	0, 1	legs III rub abdomen <sup>126</sup>	N	N	?	?	?	
<b>Ephydriidae</b>									
<i>Ochtotherus occidentalis</i> Clausen	F	9, 0	legs III rub wings	N	?	Y	N	?	
<b>Micropezidae</b>									
<i>Pilocoschus</i> sp. nr. <i>arthriticus</i> (Wiedemann)	FH	0, 6	mouthparts dab liquid on eyes legs I tap eyes, prothorax <sup>127</sup>	N	?	Y	N <sup>128</sup>	no movement	

APPENDIX Continued.

Taxon	Site of observation <sup>1</sup>	N <sup>2</sup>	Male copulatory courtship behavior pattern <sup>3</sup>	Male mounted after copulation?	Sperm emerge <sup>4</sup>	Pre-copulatory courtship?	Copulation same as precopulation?	Genitalic events	Reference <sup>5</sup>
Muscidae									
<i>Neodextopis</i> sp.	FH	0, 1	legs III rub abdomen <sup>129</sup>	?	?	?	?		
Nereidae									
<i>Glyphidops (Oncopsis)</i> sp.	CM	6, 1	legs I rub head, prothorax <sup>130</sup> genitalia tap base ovipositor	N	N	Y	Y	no movement	
Richardiidae									
<i>Richardia</i> sp.	CMV	3, 1	head vibrates dorso-ventrally <sup>8</sup> body rocks side-to-side <sup>8</sup> legs III rub tip abdomen <sup>17</sup> body rocks side-to-side <sup>8,131</sup> legs III press abdomen legs III squeeze abdomen legs III rub abdomen wings buzz	N	N	Y	N	?	MCM, WE
<i>Richardia</i> sp.	CMV	1, 2	legs III rub tip abdomen <sup>17</sup> body rocks side-to-side <sup>8,131</sup> legs III press abdomen legs III squeeze abdomen legs III rub abdomen wings buzz	N	N?	Y	Y	no movement	
Sciaridae									
<i>Bradysia</i> ?	FH	1, 0	(?) <sup>132</sup>	N	?	Y?	?	?	
Sepsidae									
<i>Paleosepsis armillata</i> (Melandier and Spuler)	FH	0, 2	no movement	N	?	?	-	?	
Stratiomyidae									
<i>Merosargus</i> sp.	F	4, 10	legs III wave at female <sup>8,98,133</sup>	N	?	N?	N	?	
<i>Merosargus</i> sp.	F	2, 2	legs III rub abdomen <sup>98,134</sup>	N	?	N	N	?	
<i>Plecticus mexicanus</i> James	F	1, 0	legs I tap head	N	?	N <sup>135</sup>	?	?	
Tephritidae									
<i>Euretra</i> sp.	FH	0, 2	wings buzz rhythmically <sup>17,136</sup>	?	?	?	?	raise tip of abdomen rhythmically small in-out movements	
<i>Paraxyna</i> sp.	CM	1, 3	legs III rub ovipositor <sup>137</sup> mouthparts tap mesonotum?	N	?	Y	Y	Y	
Hymenoptera									
Scelionidae									
Prob. <i>Telenomus</i> sp.	CM	3, 0	no movement <sup>138</sup>	N	N <sup>139</sup>	N	-	?	
Orthoptera									
Eumastaciidae									
<i>Episactus ca. tristiani</i> Rehn and Rehn	FH	0, 6	legs III vibrate <sup>8</sup>	?	N	?	?	small rhythmic movements	

APPENDIX Continued.

Taxon	Site of observation <sup>1</sup>	N <sup>2</sup>	Male copulatory courtship behavior pattern <sup>3</sup>	Male mounted after copulation?	Sperm emergence <sup>4</sup>	Pre-copulatory courtship?	Copulation court same as precopulation?	Genital events	Reference <sup>5</sup>
Mantidae									
<i>Stigmomantus venusta</i> Sauss	FCM	0, 2	body jerks <sup>140</sup>	N	?	Y	N	small movements	
Rhipipterygidae									
<i>Rhipipteryx biolleyi</i> Saussure	FCM	0, 13	no movement <sup>98,141</sup>	?	?	Y	-	rhythmic pulsing	
Trichoptera									
Philopotamidae									
<i>Chimarra</i> sp.	CM	1, 5	no movement <sup>98,142</sup>	N	N	Y	-	rhythmic movements abdomen	
Araneae									
Pholcidae									
<i>Physocyclus globosus</i>	CM	28, 0	abdomen vibrates <sup>8,143</sup> legs quiver	N	Y	Y	N	twist palpal sclerites rhythmically <sup>144</sup>	WE
Tetragnathidae									
<i>Leucauge mariana</i>	CMV	30, 0	anterior legs tap those of female <sup>145</sup> legs push those of female abdomen quivers <sup>8</sup>	N	N	Y	N	multiple intromissions of three types <sup>146</sup>	WE
<i>Leucauge</i> sp.	CH	5, 0	anterior legs tap those of female <sup>145</sup> body rocks <sup>8,17</sup> legs I, II push, vibrate on those of female or in air <sup>8</sup>	N	? <sup>139</sup>	Y	Y	multiple intromissions	
<i>Leucauge</i> sp.			abdomen vibrates <sup>8</sup> abdomen flicks sharply <sup>8,145,147</sup> legs I, II push/vibrate against those of female	N	N <sup>139</sup>	Y	N?	multiple intromissions	
<i>Leucauge</i> sp.	F	1, 1	legs II (and I?) quiver <sup>148</sup> legs IV tug web <sup>8</sup>	N	?	Y	N	multiple intromissions	
<i>Plesiometa argyra</i>	CM	1, 1	no movement <sup>145</sup>	N	N	Y	-	multiple intromissions	
<i>Tetragnatha</i> sp.	FH	0, 1	no movement <sup>149</sup>	N	?	?	?	?	
Theridiidae									
<i>Chryso</i> sp.	CH	1, 0	no movement <sup>150</sup>	N	? <sup>139</sup>	Y	N	rhythmic expansion and collapse of hematochaecae	

## APPENDIX FOOTNOTES

1. C, captivity; F, field; M, under dissecting microscope; V, video recordings; H, headband magnifier.
2. Number of complete copulations is followed by number of partial copulations; each intromission was counted as a copulation.
3. Part of male body used is followed by site on female body that was contacted.
4. Unless otherwise noted, presence of sperm in material that emerged from rear portion of female during or just following copulation was confirmed by examination at 400 $\times$ . The angle and level of detail of observations of many species precluded observations on this point. In most species classified as "Y," sperm emission was associated with some copulations but not others.
5. Report in preparation. VR, V. Rodriguez, including Rodriguez 1993, in press; RLR, R. L. Rodriguez; MCM, M. C. Marin; SL, S. Lobo; LD, L. Diaz; CM, C. Marquez; WE, W. Eberhard, including Eberhard 1993c.
6. One leg I (always on same side of a given pair, on different sides in different pairs) rapidly tapped the side of female pro- and mesothorax as leg moved forward and backward repeatedly in short bursts of activity. During bursts the ipsilateral antenna tapped on same side of female head and eye; the other antenna tapped on front of female head in some pairs, but contacted female only intermittently in others; male mouthparts tapped on female pronotum (or, when male was small, on her elytra) as male moved forward and backward.
7. Both legs III snapped ventrally simultaneously about once every 2–6 s causing female abdomen to jerk ventrally.
8. Vibrating structure not in direct contact with female, but movements sufficiently intense to be sensed by the female via other structures that contacted her and/or through web lines.
9. Male movements apparently released when female moved after a period of inactivity.
10. Male lunged forward rapidly, grasping female roughly with his legs as he bit at her with his mandibles.
11. Male mouthparts generally contacted female elytra and often quivered, moving on her as the male rocked and/or twisted her abdomen.
12. Male movements appear not to be associated with thrusting his genitalia deeper into female.
13. Rhythmic inflation of the genitalic membrane resembled the other *Chauliognathus* species. Rhythmic movements within male genitalia were accompanied by simultaneous movements of a dark object within female abdomen. The male occasionally twisted female abdomen briefly, but not rhythmically as in other *Chauliognathus*.
14. Short bursts (< 0.5 s) of body vibrations, often in series of 2–12, were often associated with movements by the female. One male vibrated legs III in the air. Mouthpart contact on female femur II was mostly limited to the first 1–2 min of the several-hour copulation. The male repeatedly dismounted without uncoupling his genitalia, and on remounting usually ran his mouthparts over female pronotum and/or elytra.
15. In all three pairs, a clear mass appeared on the male genitalia during copulation. When I pulled, a clear tube about the length of the female's entire body emerged from area of genitalic coupling (it was not clear which animal it came from). Many regular oval bodies were present around one, and a few were inside another; the third was empty. Up to 14 such spermatophores, with variable numbers of oval bodies, accumulated on the floor of containers where a pair was left for several days (most of which were spent in copula).
16. Male may have slightly twisted the tip of the female's abdomen rhythmically, but the movement was much smaller than in other species of *Chauliognathus*.
17. Did not occur in some copulations.
18. Sperm emerged from female as male genitalia were withdrawn.
19. During bursts of brisk rocking movements male genitalia made rapid, shallow thrusts, the mouthparts rubbed vigorously on the female's elytra, and the antennae usually tapped on the sides of female pronotum. Genitalic thrusting also occurred between bouts of rocking.
20. Genitalic thrusting movements were much more rapid and numerous than in related *Macrohaltica* (Eberhard and Kariko in prep.). During each thrust, male mouthparts contacted female elytra, perhaps to gain purchase. Legs III tapped the female during bursts of genitalic thrusting: they were raised, extended laterally, then swung ventrally so their tibiae hit the ventral surface of the female's abdomen. Antennal taps on female elytra occurred in short, infrequent bursts along with brisk seizures of the female with male legs. Bursts of movement occurred only during periods of rapid, numerous (up to 85) genitalic thrusts. Antennal vibration occurred briefly just as the male began each genitalic thrust.
21. Sperm emerged after male withdrew his genitalia.
22. Only occurred after copulation ended; male left without attempting further intromissions.
23. Male antennae were always extended anteriorly over female eyes at the start of a burst of vibrations; they touched female eyes at the end of at least some bursts.
24. Male antennae vibrated as they swept back and forth over the female; tarsi II shifted back and forth many times on female elytra and also quivered rapidly. Male legs III were on the substrate, and by repeatedly extending them briskly, often in rapid series, he caused his body (and because of his rigid genitalia, that of female) to jerk dorsally.
25. Antennal movements were similar to those of *Brachyopaoea* cf. *irazuensis*. Leg II movements differed in usually occurring in series of progressively more rapid taps that culminated in the leg being extended somewhat as the femur rubbed rapidly forward and backward on the female's elytra.
26. Male made repeated short dashes forward, sideways, or backward over the female with his mouthparts touching her. Some forward dashes ended with male mouthparts close to the base of female leg; in one case he seized the leg briefly with his mandibles.
27. Rhythmic thrusts of genitalia, each preceded by

- movement of genitalic structures within male phallobase toward female, occurred early in copulation. Later thrusts were shorter, shallower, less frequent, and irregularly spaced. Bursts of side-to-side rocking, sometimes weak, occurred both immediately preceding thrusts and later. Because the male's abdomen was relatively rigid, rocking may have stimulated female external genital opening. Sperm were emitted following first copulation in only pair in which male remained mounted and copulated a second time (following which he dismounted and walked away).
28. Sperm emerged while male genitalia were within the female.
29. During first portion of copulation structures within male phallobase (probably his internal sac) moved into female just as each thrust began then slowly reemerged after the thrust. After thrusting ceased, these structures were not visible inside the phallobase and were presumably inside the female.
30. During most of the several-hour copulation, the male often made small rhythmic genitalic thrusts about once/10–20 s. At intervals of 6–22 min, the male moved abruptly forward on the female, pulling the tip of her abdomen dorsally with his genitalia while he rapidly tapped the sides of her prothorax with alternate strokes of his antennae for about 10 s. Occasionally male tapped without moving forward.
31. Movements of material within male genitalia toward female and back out also occurred in a rhythm different from that of thrusting movements.
32. Female vibrated body repeatedly during first 30 min of a 99-min copulation. The male tapped the female on head and elytra with legs I just before intromission, and during 20–30 s just prior to ending intromission and leaving her.
33. Female genital opening opened and closed rhythmically.
34. Approximately 1-s bursts of activity began when male antennae vibrated quickly; he then lunged forward and ventrally, and wiped his mouthparts rapidly from side-to-side on female elytra as he tapped her antennae with his. In three pairs, the male simultaneously rubbed his legs III on the female's venter.
35. Body vibrations occurred independently of other behavior.
36. After withdrawing his genitalia, male moved forward on female dorsum, leaned laterally, and mouthed female femur II 2–5 times. At the same time, he stridulated, rubbing the tip of his abdomen against the tips of his elytra (sound production by these movements was verified directly with beetles held in forceps).
37. Mating in three of four pairs included multiple intromissions.
38. Rapid thrusting lasted for first 20–40 s of intromission. Depth of thrusts varied from about one-fourth to entire length of male phallobase. Part of internal sac (visible through the semitransparent walls of the phallobase) moved into the female at the start of each thrust. It remained inside after thrusting ended when the phallobase was held deep in female.
39. Male tarsi III rubbed slowly and persistently across the ventral surface of tip of female abdomen, generally in forward-backward directions but sometimes laterally.
40. More thrusts occurred in each burst than in two other *Macrohaltica* species (Eberhard and Kariko in prep.).
41. A chittering sound occurred during copulation, but it was not clear which individual produced it.
42. During most of copulation male abdomen slid rhythmically back and forth over the shaft of the immobile phallobase as in some weevils (footnote 61); late in copulation some movements produced an in-out movement of the phallobase in female.
43. Male defended area where female oviposited.
44. It was not clear whether the stimulation criterion (male movements appropriately designed to stimulate the female) was fulfilled.
45. Also performed 40–50 s before intromission ended.
46. Both during and after copulation.
47. Male tarsi I and II slipped repeatedly on the female elytra in such an irregular pattern that courtship seemed unlikely.
48. Repeated bursts of scraping were audible; vibrations were also perceptible when I held a leaf with mating beetles in my fingers.
49. Legs I and legs II pushed laterally and rubbed across female elytra. Legs III rubbed ventral surface of female abdomen.
50. A burst of rubbing began with a quick jerk produced by a quick flexion of legs III. Male mouthparts also contacted female.
51. "Thrusting" resulted in telescoping of terminal female abdominal segments.
52. Most rubbing occurred between intromissions or just before the male withdrew his genitalia.
53. Both side-to-side and dorso-ventral movements.
54. While attempting intromission, male sometimes tapped rapidly on female elytra with his mouthparts. Similar rapid tapping occurred for 2–8 s after intromission ended, just before male dismounted. Legs III of male vibrated continuously during 1–3 min copulation. They were raised, but touched near edges of female elytra repeatedly.
55. Genital rod or rods (parameres?) vibrated weakly on female abdomen during part of 1–2 min copulation.
56. Rubbing also occurred after copulation. In one of five copulations male vibrated his legs III briefly as in *Epilancha borealis*.
57. A mounted, noncopulating male in field performed rubbing movements; copulation in captivity not preceded by courtship.
58. Male parameters were spread in a "V" and rested on or very near ventral surface of female abdomen. They did not move except to clap together once just before the male cypho emerged at the end of the approximately 30-s copulation.
59. Mouthparts touched female when they moved, but movement was not rhythmic; similar contact plus antennal tapping occurred prior to intromission. In eight cases, male remained mounted briefly on female after withdrawing his genitalia and ran his mouthparts over her elytra moving them rapidly as he did so.

60. Periodically male moved forward and laterally on female for 1–2 s. His lower leg III rubbed the ventral surface of her abdomen, and upper leg III rubbed her pygidium. His body jerked, causing his mouthparts to rub on her elytra, and he apparently stridulated by rubbing the dorsal surface of his abdomen repeatedly against the tips of his elytra.
61. The most common movement was repeated about every 10–20 s: after sliding slightly forward on female, the male pulled his pygidium away from her, exposing the basal portion of the phallobase and a clear sac there. Then he moved his pygidium toward female and pushed his genitalia forward into her as his thorax moved slightly rearward. Other genitalic movements included quick ventral flexions of tip of male abdomen, driving the curved phallobase dorsally within female.
62. No sound was heard. The tip of the male abdomen vibrated rapidly dorso-ventrally against tips of male elytra in a way associated with sound production in other contexts.
63. Movement caused male ventral surface to rub female dorsum.
64. In one copulation interrupted when the beetles were captured, there was sperm in the spermatophore that emerged as the male withdrew his genitalia; in the other, which terminated naturally, no sperm was found in a similar spermatophore.
65. Male meso- and metasterna rubbed on female as he moved forward and backward. Male rostrum was in contact with female nearly continuously, except during genitalic thrusts. Occasionally his mouthparts moved for up to 3 min while in contact with the female. Small side-to-side taps with the beak occurred in series of up to 10.
66. A mass of viscous material adhered to tip of male genitalia when they were withdrawn; no sperm were visible at 400 $\times$ .
67. Stridulation, when tip of male abdomen rubbed rapidly back and forth against his elytra, was verified by listening through a rubber tube placed near a copulating pair.
68. Male repeatedly clasped female strongly, enclosing her head, prothorax, and anterior legs with his legs I, whose ventral surfaces differed from those of the female in having dense covering of short setae. Repeated postcopulatory clasping occurred in two of three pairs.
69. Legs also moved rapidly, and legs II may have rubbed female, but movements were relatively uncoordinated (in contrast with the behavior of the Costa Rican form; see footnote 73).
70. A small mass of white material that emerged from male abdomen when copulation ended was not checked for sperm.
71. Male beak rubbed female pronotum briskly from side to side during copulation; before intromission he rubbed her head and beak in a much more variable pattern.
72. Sometimes male abdomen moved as described in footnote 61. Other times, male abdomen made shorter, quicker movements that did not expose the sac near the base of the phallobase.
73. Male legs III were periodically extended posteriorly and vibrated rapidly dorso-ventrally; this behavior almost always immediately preceded short bouts of rapid rubbing and tapping on female abdomen with legs III mostly dorso-ventrally and on her elytra and pleura with legs II (mostly antero-posteriorly).
74. In one pair, the male waved his legs just before he withdrew his genitalia, then left. In another, waving occurred just after the male withdrew; during the next 10–15 s he pressed his beak to the female and applied his genitalia briefly to those of the female, then left (in contrast with prolonged genitalic contact lasting up to 15–20 min during precopulatory courtship).
75. At first, the male thrust his phallobase rhythmically deep into the female. Then structures within the phallobase (probably the internal sac) moved into the female, and he switched to moving tip of his abdomen back and forth over phallobase (see footnote 61) during the rest of the several-hour copulation. In some cases, a small movement of the phallobase into female occurred as male abdomen moved rearward. In two cases, the male withdrew from the female within 5 min, in one immediately after the membranes inside the phallobase moved toward female and in the other before.
76. Genitalic movements occurred in bursts lasting 3–4 min. At the start of several bursts of thrusting, the male performed one to eight convulsive flexions of his legs, especially III that held the ventral surface of the female's abdomen.
77. Sperm emerged while male genitalia were in the female in 10 of 20 copulations lasting longer than 6 min.
78. Male tarsi III and tips of tibiae III jerked ventrally rhythmically during bursts of activity. The male simultaneously raised the female's body slightly with his legs I and II.
79. Prior to intromission, male slid his extended genitalia forward along or under the edge of female elytra three times.
80. Male mouthparts rubbed briskly from side to side on the female's pronotum before, during, and following the approximately 2-min copulation. Following two copulations, the male moved forward on the female, performed more mouthpart rubbing that seemed different from that during copulation (included mandible contact?), and pressed the female head ventrally with ventral surface of his several times. He then rubbed the female's dorsum with his mouthparts as he dismounted.
81. Pair of male genitalic processes also tapped on the tip of the female abdomen for about 30 s just before intromission.
82. Male rocked entire body from side to side often in bursts of about 5–10 rocks.
83. This species differs from *Macroductylus costulatus*, *M. sericinus*, and *M. sylphis* (Eberhard 1993): neither vibrations of legs III, nor extension of the antennae to cover the female's eyes or rub her prothorax while the head is vibrated occur in the other species; blows with legs II to female near her antennae were short and rapid rather than longer "swings."
84. Rhythmic movements of structures inside male phallobase were coordinated with displacements of structures within female; thus, male genitalia probably thrust rhythmically in female.

85. Portions of male sternites that rub female pygidium are often species-specific in form in this genus (Morón 1986).
86. Rhythmic movements of male genitalia, which slid inward and outward in female genitalia, were probably caused by genitalic movements inside female (Eberhard 1993c).
87. Rubbing occurred in bursts. Anterior margin of male head contacted female scutellum during nearly entire 10 min of copulation.
88. A mirror placed underneath the insects was used to observe ventral surfaces.
89. Prior to copulation, male sometimes tapped female with mouthparts, also rubbed antennae along sides of female pronotum. During copulation, mouthpart contact ceased. Male mouthparts were pressed against female elytra whenever she began to walk.
90. Contractions of male genitalia caused a pair of long genitalic sclerites to rub rhythmically across latero-dorsal surface of tip of female abdomen.
91. Female first seen with a male mounted but not copulating deposited a pair of small, clear objects on the substrate: the male, presumably having copulated, then dismounted and left. At 400× each object consisted of a pair of more or less spherical structures, one larger than the other; both pairs had 30–50 “spinelike” objects (sperm?) embedded in an amorphous mass.
92. Sexually dimorphic fringe of long hairs on male venter spread on female elytra while the male was mounted. The small rocking movements of male accompanying rhythmic genitalic contractions (about 1/s) caused hairs to rub slightly on the female.
93. Spasms of rapid movements suggested stridulation. Movements preceding copulation were smaller and in shorter bursts of fewer movements, whereas those during copulation were at times continuous.
94. In all but one pair, male twitched his head continuously about 5 s after the 20–30 s copulation began, as when tapping female abdomen or elytra during precopulatory courtship. In four of six copulations, male mandibles touched female elytra or pronotum as he twitched his head; in all pairs, his head was in the female’s view (these are visually responsive animals). One male twitched his head repeatedly against the female’s elytra following mating.
95. Unclear whether male or female produced the movements.
96. Intromission lasted only 3–5 s; the male then withdrew, dismounted, and walked away.
97. Male genitalic style rubbed female rhythmically.
98. Copulate in tail-to-tail position.
99. After about 1 h of copulation, a clear, viscous mass (not checked for sperm) formed at base of ovipositor.
100. Rhythmic extensions and retractions of the male’s style averaging about 1/7 s, occurred continuously for 15–30 min at a time. A rhythmic back-and-forth flow of material was also visible inside the semitransparent male genitalia; each time material apparently flowed into female, the ventral surface near the tip of her abdomen swelled slightly. In-out cycles lasted about 2–8 s.
101. A large, oval opaque white mass formed at the base of the female’s ovipositor during copulation. Some otherwise immobile “hairs” emerged from the mass, and many later withdrew again.
102. Male legs (folded against his body, out of contact with the substrate during tail-to-tail copulation) repeatedly vibrated briefly, perhaps part of aborted movements to contact substrate.
103. Bursts of gentle, “fluttery” tapping with one leg II and both legs I were consistently elicited when the female moved and when another bug moved nearby. Similar taps occurred when the male climbed onto female dorsum after copulation ended.
104. Sharp body jerks occurred occasionally, but it was not clear which individual was responsible.
105. Most of the time, bugs were tail to tail, but the male periodically turned nearly 180° and tapped the female dorsum with his antennae for 1–2 s. Toward the end of the tapping, the male’s beak was extended, and touched the female head and/or prothorax several times. One exceptional burst of tapping with the beak lasted about 60 s. The distal portion of the male genitalia lodged firmly in tip of female abdomen, and rapid, sustained twitching of the articulation between his genital capsule and his abdomen (about 5/s) caused her body to vibrate.
106. Both legs were raised simultaneously, and their tarsi rubbed the rear third of female abdomen; during the first 5–10 min of copulation, male periodically pushed female abdomen with tibiae of legs III pulling his genital capsule partly away from the rest of his abdomen. Occasionally a male turned to rapidly mount the female and tap her rapidly with his antennae, then immediately dismounted. The female waggled her abdomen nearly continuously from side to side with increasing force during the last three quarters of the approximately one hour copulation.
107. Genitalic movements included small but nearly continuous movements of parameres that deflected hairs on the female’s abdomen, and occasional movements of material within male genitalia.
108. Male legs III often touched female abdomen and wings repeatedly, but slowly, tentatively, and in variable patterns.
109. Both hind legs pushed simultaneously on rear of female abdomen, separating the tips of male and female abdomens momentarily. Often one leg pushed while the other tapped or was repositioned repeatedly on female. Low amplitude body vibrations apparently involved flexion at the thorax-abdomen articulation, which displaced female abdomen rapidly dorso-ventrally. The male’s aedeagus contracted each time he pushed female with his legs III. Parameres vibrated rapidly in bursts, causing the long setae at their bases to rub on ventral surface of tip of female abdomen. Male genital capsule moved rhythmically in bursts also rubbing against female abdomen.
110. Taps occurred in short bursts. The male raised both legs III, brought them toward the female, then gave her abdomen one to five soft brisk taps, usually with both legs simultaneously.
111. Bugs observed near La Planada, 8 km south of

Ricaurte, Nariño, Colombia. Side-to-side rocking movements occurred periodically, but it was not clear whether the male or female was responsible. Interruption of female cleaning, repositioning of female legs just after the start of shuddering, and extension of the male legs III just prior to shuddering suggested that male rather than female produced shuddering bouts. Bouts occurred at intervals of about 1–5 min and lasted 5–10 s. Most shuddering movements were lateral. Intensity increased during each bout, and male elevated the tips of his and female abdomen (female sometimes struggled for a foothold). Usually only one tarsus III tapped on ventral surface of the female abdomen at a time, with dorsal surface touching during the small, rapid taps. Occasionally one leg III brushed quickly across the dorsal surface of tip of female abdomen.

112. Bugs observed near San Antonio de Escazu, San José Province, Costa Rica. No body vibration or shuddering was seen as in Colombian *Mormidea notulata*. Low amplitude dorso-ventral abdomen vibration was rapid causing abdomen to blur. Bursts of vibration during precopulatory courtship were longer (up to about 1 s) than during copulation (about 0.1 s). In contrast to the behavior of Colombian bugs, clearest tapping behavior occurred soon after genitalic coupling and less often and in less elaborate form during rest of approximately 8-h copulation.

113. Tapping differed from *Mormidea* sp. n and Colombian *M. notulata* in being concentrated on the legs and the lateral rather than the ventral portions of the female abdomen.

114. Usually ventral surfaces of all segments of tarsi III were brushed backward-forward in rough alternation about once every 1–2 s on the ventral surface of the female abdomen, but details varied. Rubbing was more or less continuous for up to 15 min. The bugs' bodies also rocked side to side periodically (see footnote 111). Male sometimes jerked or vibrated legs III, sometimes touching female legs III or pronotum. The female may have sensed visually movements of the male's legs.

115. Tapping during the tail-to-tail copulations occurred in short bursts (0.5–3 s) after long pauses (3–15 min). The male rapidly tapped and rubbed both legs III on posterior surface of female abdomen. The male also repeatedly rubbed one leg III over dorsal surface of his pygofer and against female wings and abdomen. The dorsal surface of the pygofer became moist, and some liquid was transferred onto the female. Three of four females vibrated their bodies laterally (in two cases nearly continuously for the first hour of the several-hour copulation) and occasionally rubbed male genitalia with one hind leg.

116. Timing of tapping behavior varied between species.

117. Frequent sustained small side-to-side rocking movements (about 1/s) may have been associated with genitalic movements (genitalia were not visible).

118. Each time, the male leaned back after tapping, his legs twitched about three times as he withdrew them. Nearly all 32 bursts of tapping during one

290-min copulation were followed by twitching. No stridulation was observed.

119. A clear, viscous substance (not checked for sperm) was on the tip of the male genitalia after one brief copulation.

120. No sound was heard. The head vibrated rapidly dorso-ventrally, with tip of rostrum in striate sulcus between coxae I just before most (all?) bursts of tapping. Similar head movements produced sound when I held a bug in forceps.

121. Membranous portion of genitalia pulsed slowly. No stridulatory or twitching behavior was observed.

122. In precopulatory courtship male rubbed his genitalia near female genital opening.

123. The male was alongside female, with leg II and leg III nearest female across her dorsum. In bursts of scrubbing movements, leg II rubbed her dorsal surface and leg I her ventral surface.

124. One behavior sequence was repeated in three of four pairs: once every 1–4 min male bent and twisted the tip of his abdomen laterally causing female abdomen to extend. After about 1 s, he moved tip of his abdomen back and forth jerkily with less severe flexions for several seconds; finally he jerked the female rearward with a series of 3–4 sharp ventral flexions of the tip.

125. Precopulatory courtship occurred after pair formed in midair and dropped to ground. Male genitalia rubbed and tapped on those of female in bursts (1–2/s).

126. Rubbing varied during copulation. For about 3 min it was nearly continuous and slow (about two strokes/s); then it ceased (about 8 min); finally (last 3 min) more rapid strokes occurred in short bursts.

127. After the male leaned forward to place a droplet of clear liquid on female eye with his mouthparts, she immediately wiped it off with ipsilateral tibia and tarsus I, then wiped this leg with her mouthparts. Often male rubbed female eyes and/or prothorax with legs I in several bursts between droplets. Right and left legs rubbed with jittery movements in quick alternation during a burst. One male deposited 35 droplets in approximately 10 min.

128. One solitary male had a clear droplet on mouthparts for about 1 min, then reingested it.

129. Male legs III rubbed briskly near the ventral midline of the female abdomen once or (less often) twice every 1–2 s.

130. Most leg I taps during precopulatory courtship hit the female head and antennae; taps during copulation were on her thorax. Genitalic tapping was of two types.

131. Rocking occurred in bursts. The male leaned forward and then rocked sharply from side to side. In some cases, rocking was strong enough to cause female to momentarily lose her foothold with one or more legs. Male also pressed rhythmically on female abdomen with his legs III. Tips of tibiae III rested together on ventral surface of her abdomen just anterior to ovipositor, and each press caused the tip of the tibia to become more deeply embedded in the folded cuticle of the female abdomen. Pressing occurred in bursts. Squeezes also occurred in short series; the male briefly opened the tibia-

- femur clamp of both hind legs on the female's abdomen then sharply closed it again. Squeezing often preceded a bout of rocking. The male rubbed the female abdomen by repeatedly raking his legs III forward to the base of her wings. The femur apparently brushed the dorsal surface of her abdomen, the tibia the ventral surface.
132. Postcopulatory behavior was perhaps not directed toward the female. Male stood beside female for about 1 s after uncoupling genitalia then began buzzing his wings and walked around on the leaf. His abdomen was not bent forward as during courtship, and there were no other flies on the plant. The female flew to a leaf about 30 cm away, and the male continued to buzz and walk for 5–10 s, hovered nearby then landed again on the same leaf and ran briefly and buzzed. I then collected both animals.
133. Coupling occurred in flight. After pair landed (tail to tail), male raised legs III repeatedly over his abdomen. Details of leg movements varied; the most elaborate were alternate waving movements over male abdomen. In three pairs, the male buzzed his wings briefly taking to the air briefly while tethered by his genitalic connection with the female.
134. The male repeatedly rubbed his legs III together vigorously as if cleaning them brushing sides and or the ventral surface of the female abdomen. About once every 10 s he paused, raised both legs III simultaneously then began rubbing again.
135. Leg I taps probably occurred only after genitalic coupling, but this could not be verified since coupling began in midair.
136. In one pair, male buzzed wings 5–6 times rhythmically (about 1 burst of buzzing/s). The pair (the female?) immediately flew to a more sheltered perch. The male legs I appeared to stroke anterior portion of the female abdomen repeatedly while he buzzed.
137. Rubbing prior to copulation was mostly on the sides and dorsal surface of female ovipositor and at times appeared to constitute gentle attempts to raise her ovipositor for allow seizure with male genitalic claspers. Energetic rubbing during copulation was on ventral surface of ovipositor.
138. In two pairs, male antennae began moving near the front of female head during approximately the last second of 3–4 s copulation, perhaps in anticipation of climbing off. Male antennae were motionless during the third copulation.
139. Copulations with virgin females only.
140. Male antennae were directed forward during brief bursts of forward-backward body jerking; they sometimes appeared to contact the female.
141. Pairs often rocked forward and backward; judging by observations of males losing footholds during rocking, females moved males rather than vice versa.
142. Female legs III made repeated bursts of quivering taps on male posterior. Peristalsis within male transferred white material to female for about 60 s near the end of 15–20-min mating.
143. The male clasped female genital plate with chelicerae, contacting female with species-specific bristles and knobs on chelicerae.
144. Rhythm of movements changed in consistent ways during copulation.
145. Females of *Leucauge* species and *Plesiometta argyra* clasped male chelicerae with their own chelicerae, thereby contacting the often species-specific area of bristles on male chelicerae. Tapping usually occurred as one palp was removed and the other inserted in female genital opening. In *Leucauge mariana*, tapping was also common while palp was inserted. In Colombian *Leucauge*, most tapping was with legs II; similar tapping did not occur in species from Panama and Australia.
146. The male apparently attempted to deposit sperm plug during later stages of copulation but often failed.
147. The abdomen flipped ventrally with single, strong movement, differing from the smaller amplitudes and often multiple movements of other *Leucauge*. In all three species, abdominal vibrations caused visible vibration of female.
148. Dorsal surface of each male leg pressed against ventral surface of corresponding female leg (leg I on leg I, etc.).
149. The front legs tapped for about 1–2 s just before the male withdrew, and female spread her legs I in apparent response. This behavior may thus function to induce the female to allow male to escape rather than to use his sperm. During copulation, the male held female chelicerae open with his chelicerae.
150. Both spiders' bodies jerked sharply 3–4 times simultaneously just before they separated. I could not tell which spider was responsible for the movements.